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DISCRIMINATION BETWEEN REGIONAL SONG FORMS IN THE NORTHERN PARULA

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ABSTRACT.—Distinctly different territorial (Type A) song forms characterize western and eastern populations within the breeding range of the Northern Parula (*Parula americana*). We conducted playback experiments to determine if territorial males respond differentially to the two song forms. Male response is stronger to Type A songs of their own population than to the songs of the other population (two-tailed Wilcoxon test, $P < 0.001$). The possible basis for this discrimination is discussed. *Received 3 Dec. 1993, accepted 15 Oct. 1995.*

Many oscine species exhibit geographic song variation (Thielcke 1969), and some of these species' songs vary microgeographically, with two or more small scale local dialects (Kroodsma 1981, Tomback et al. 1983, Kroodsma et al. 1984). In species such as the Mourning Warbler (*Oporornis philadelphia*), there is macrogeographical song variation, with two or more distinct and widespread regional song forms or song populations (Pitocchelli 1990).

The Northern Parula (*Parula americana*) has two primary song types, Types A and B (Moldenhauer 1992). Spectrographic analysis of Type A songs from throughout the breeding range by Moldenhauer (1992) revealed an eastern and a western song population (Fig. 1) whose songs are characterized by distinctly different terminal notes (Fig. 2). Playback experiments have shown that in species whose song varies geographically, territorial males can often distinguish between different dialects or song forms, as inferred from the intensity of response to playback (Kroodsma et al. 1984, Ritchison 1985). Usually, the response is stronger to local or familiar song forms. In the present study we conducted playback experiments with eastern and western Northern Parulas to determine if territorial males would respond differentially to eastern and western forms of the Type A song.

METHODS

Our experimental design and data analysis follow Kroodsma et. al. (1984) and Kroodsma (1989), with certain modifications. We obtained over 100 Northern Parula Type A songs from the Texas Bird Sound Library (TBSL) at Sam Houston State Univ. in Huntsville, Texas, the Cornell Library of Natural Sounds (CLNS) at Cornell Univ., and The Borror Laboratory of Bioacoustics (BLB) at The Ohio State Univ.

We used REAL TIME SPECTROGRAM software (by Engineering Design, Belmont, MA) to measure the trill portion of each song for two characteristics: trill duration (TD)

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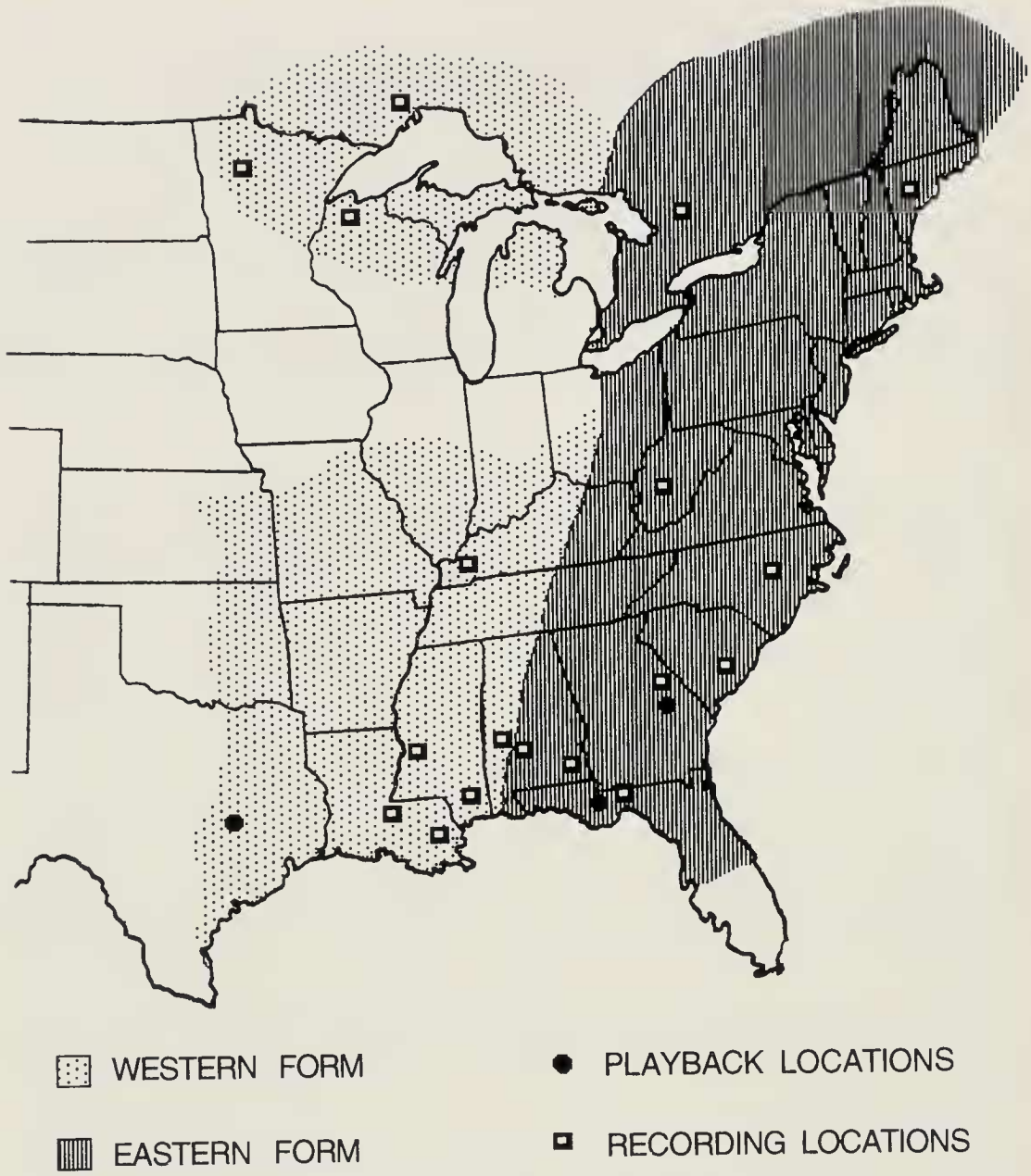

FIG. 1. Map of the distributions of the western and eastern song populations within the breeding range of the Northern Parula, as well as the recording locations for the songs used to make the playback tapes and the locations of the playback experiments.

and trill rate (TR), the number of trill syllables per second. The trill is the portion of the song preceding the last syllable or terminal note. The eastern and western populations differ significantly in the mean values for these two variables (Moldenhauer 1992). Two values were calculated for each song: TD/mean TD and TR/mean TR, using the mean values for the appropriate song population as reported by Moldenhauer (1992). The songs were arranged into pairs of one eastern and one western song that were matched as closely as possible for the values of TD/mean TD and TR/mean TR, to pair songs that were similar to one another, while taking into account the characteristics of each of the two song populations. Using this method, 12 playback tapes were made, using songs recorded at various

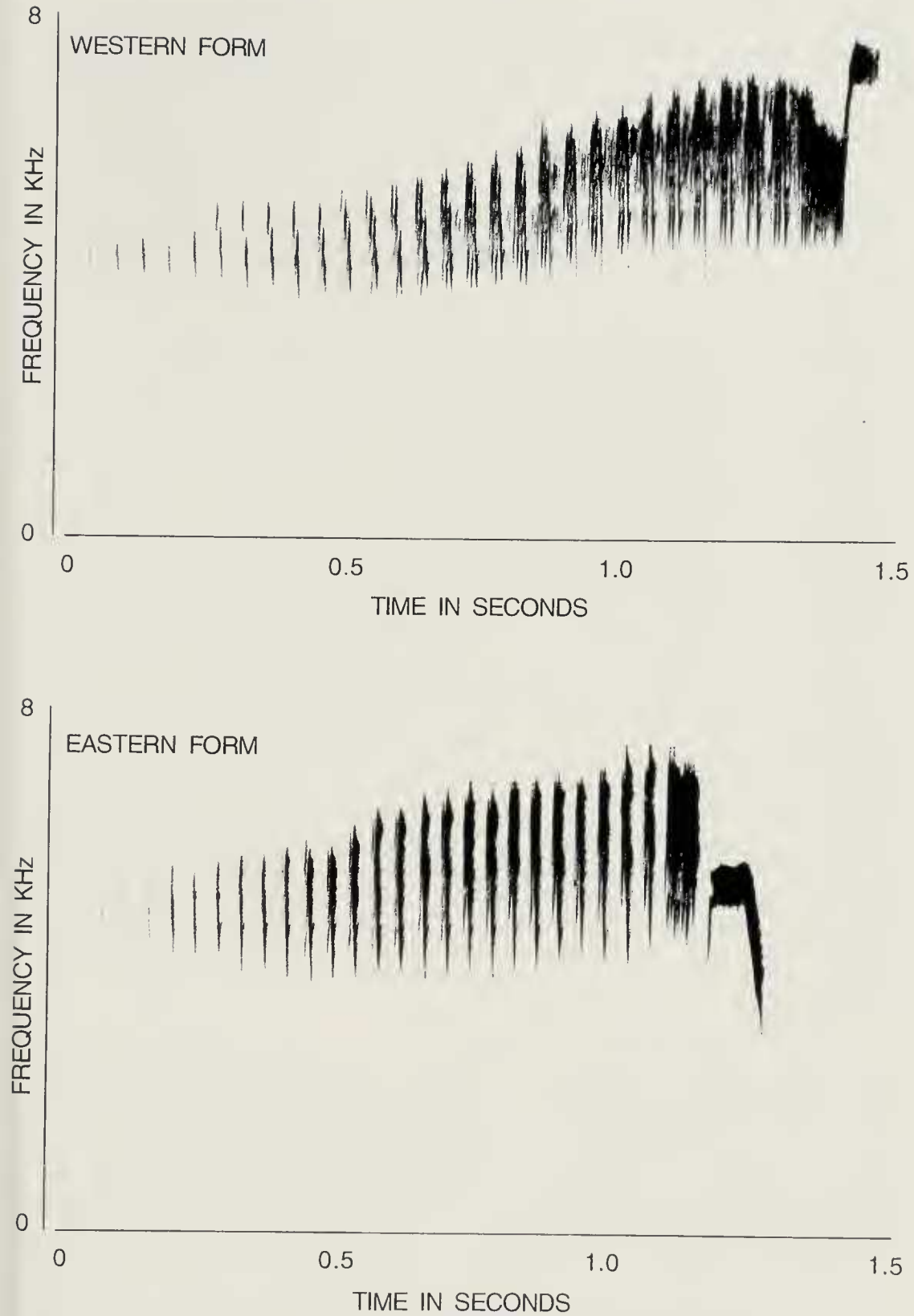

FIG. 2. Representative western and eastern forms of the Northern Parula Type A song. Notice the difference in the terminal note. These songs were used to make playback tape number 10.

dates from throughout the ranges of the two song populations (Fig. 1). Each tape consisted of 25 repetitions of one eastern song spaced 12 sec apart on the right channel, and the same treatment of one western song on the left channel. The two channels were staggered by 6 sec so that a song was broadcast from alternating speakers every 6 sec. On half the tapes an eastern song was broadcast first, on the other half, a western song was broadcast first. From 9 April to 14 May 1993, playback experiments were conducted with 12 western males near Huntsville in Walker County, Texas. From 19 to 24 May 1993, playback experiments were conducted with 12 eastern males in Liberty County, Florida, as well as Bulloch, Camden, Jenkins and Screven Counties, Georgia (Fig. 1). The same 12 tapes were used for the playbacks to both western and eastern males. This reciprocal design is discussed in Kroodsma (1989).

Songs were played on a Uher 4200 tape recorder through a pair of Radio Shack Minimus 0.8 self-amplified speakers placed 18 m apart. The playback level was set by ear to approximate a singing bird. Ribbons were placed every 2 m between the speakers, and the location of the bird during the playback period with respect to the measured 18 m was recorded every 6 s. After the first 5 min. playback period with the western song broadcast from position 0 m and the eastern song from position 18 m, the speaker cables were switched and the tape played a second time.

For the western trials, the median position of the bird during the first playback period was subtracted from the median position during the second playback period. For the eastern trials, the median position of the bird during the second playback period was subtracted from the median position during the first playback period. Positive values for difference in median positions (measured in meters) indicate a closer approach to and/or more time spent in proximity to the speaker broadcasting the bird's own song form, while negative values indicate a closer approach and/or more time spent in proximity to the speaker broadcasting the other song form. Comparing two positive values, the larger reflects a closer approach and/or more time spent in proximity to the speaker broadcasting the bird's own song form than the smaller value. Kroodsma (1989) suggests that such differences in median positions can be used as an "index of response" to the two stimuli. The greater the positive difference in median position, the stronger the response to the bird's own song type. The rationale for this method is presented by Kroodsma et. al. (1984). Therefore, we interpret closer approach to, and more time spent in proximity to a speaker broadcasting a song form, as evidenced by the difference in the bird's median position during two playback periods, as a stronger aggressive response to that song form. Hereafter, we will use the terms "stronger response" and "responded more strongly" to reflect this interpretation. Trials where the male did not approach and spend time between the speakers were not included in the analysis.

RESULTS

Ten of twelve western birds responded more strongly to their own song form, and two responded more strongly to the other song form. The bias in response is significant (two-tailed Wilcoxon test, $T_S = 8$, $P < 0.05$). Nine of twelve eastern birds responded more strongly to their own song form, and three responded more strongly to the other song form. The bias in response is significant (two-tailed Wilcoxon test, $T_S = 12$, $P < 0.025$).

To justify pooling both data sets, we compared the means of the differences in median position, a measure of the average strength of response for all 12 subjects to their own song type. These values, 4.48 m for western birds and 3.78 m for eastern birds, are not statistically different

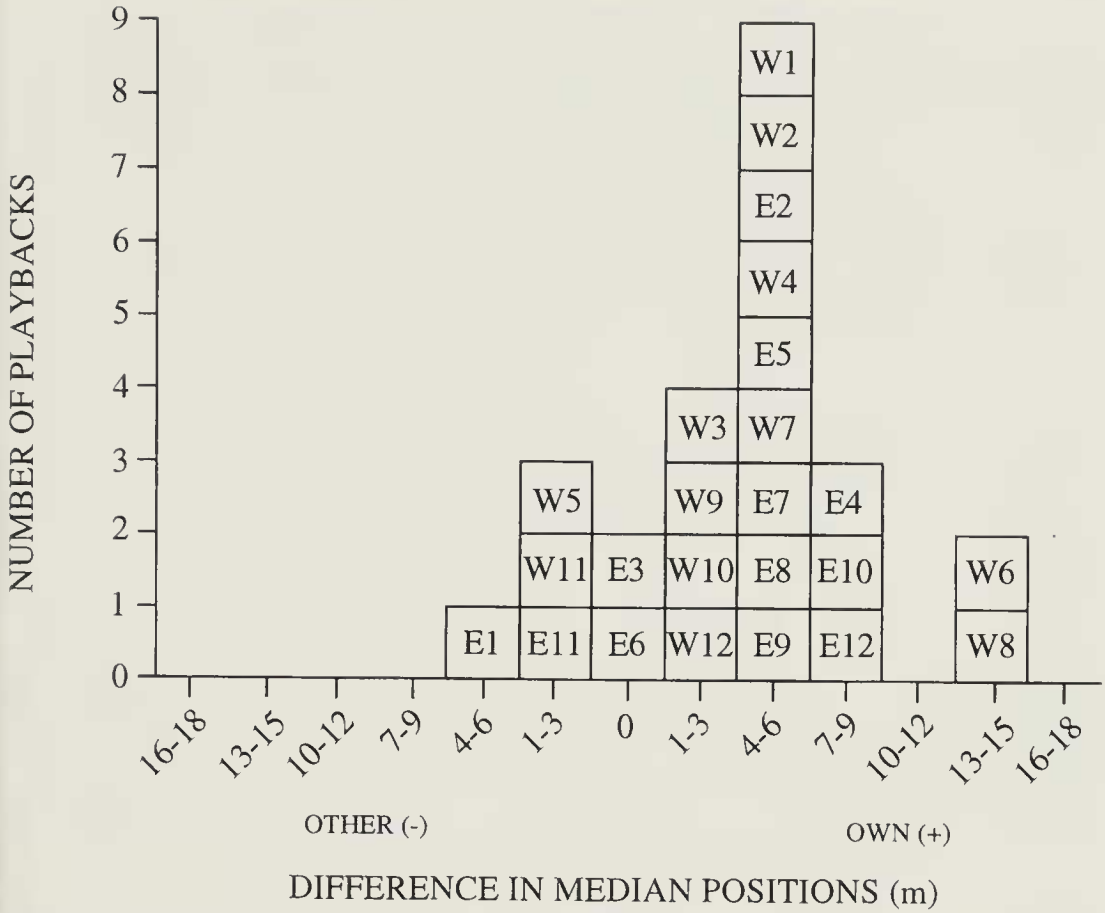

FIG. 3. Summary of all the playbacks to Northern Parulas. Each cell represents a playback session to a different male. The letter in each cell indicates whether the playback was to a (W)estern or (E)astern bird, and the number is the playback tape used. The playbacks were conducted in Texas, Florida, and Georgia. The abscissa is the difference between the median positions during the first and second playback periods. Positive values reflect a stronger response to the subject's own song form, a negative value reflects a stronger response to the other song form, and zero (0) indicates no preference. Note: for this figure, the median differences were rounded to the nearest whole number.

(two-tailed Mann-Whitney U-test $P > 0.20$). Applying Bonferroni's Inequality (Lehman 1991), the α for the test of the pooled data cannot exceed 0.049. Pooling the data gives the following results: 19 out of 24 birds responded more strongly to their own song form, and five out of 24 responded more strongly to the alternate song form (Fig. 3). The bias in response is significant (two-tailed Wilcoxon test, $T_S = 35$, $P < 0.001$). These results suggest that the birds respond more strongly to their own song form.

DISCUSSION

Territorial male Northern Parulas respond to both regional forms of the Type A song but seem to be able to discriminate between the two, as

evidenced by stronger response (closer approach, more time spent in proximity) to playback of their own song form. This resembles the pattern of response that has been observed in the Chiffchaff (*Phylloscopus collybita*), a species with macrogeographic song variation comparable to that of the Northern Parula (Thielcke and Linsenmair 1963).

In Song Sparrows (*Melospiza melodia*), the strength of response to playback of various songs increases with similarity to the subject's own song (McArthur 1986). There is also evidence that the learned association of song with aggressive behavior or territorial disputes (Payne 1986, Richards 1979) or visual stimuli (Crook 1984, Murray and Gill 1976) is involved in song form discrimination.

The two Type A song forms of the Northern Parula are relatively similar (Fig. 2), and the song probably is partially learned (Kroodsma and Baylis 1982). It is unlikely that any of the subjects had been exposed to the other song form on the breeding or wintering grounds, as the playbacks were conducted in areas of allopatry, and preliminary evidence suggests that the two song populations may have separate wintering grounds (Moldenhauer, unpubl. data). Thus, the song discrimination reported in this paper may be a result of (1) stronger response to the more structurally similar song form, (2) association of the bird's own song form with territorial disputes or aggressive interactions, (3) association of the bird's own song form with visual stimuli, such as conspecific plumage, or (4) some combination of the above. Determining how the song discrimination reported here affects gene flow in this species will require further study, especially in the area of female choice between song forms.

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